Dynamics and expansion of populations of stored product beetles

Z. Ciesielska*

Abstract

Dynamics and activity of populations of *Oryzaephilus surinamensis* (L.), *Sitophilus granarius* (L.), *Sitophilus oryzae* (L.) and *Rhyzopertha dominica* (F.) were investigated. Experiments were conducted in different environmental conditions, in single species cultures and in interspecific competition, in conditions of unidirectional emigration to jars having a glycerine trap and two-directional migration into a jars with grain. All the experiments were carried out at 27°C and ca 70% r.h., in 5–10 and 20–25 repetition.

It was shown that the level and changes in population number are influenced by environmental conditions and the population and interspecific relationships. One of the ways of regulating the population number was through change of sex ratio. The populations of all the investigated species showed high tendencies to migration and dispersal, with indices of migration from 60–80%. Migration was especially high in the initial period of attack of new habitat and in interspecific competition.

Introduction

The dynamics of an ecological system (including a population) can be forecast on the basis of the attributes of its elements (individuals) or on the basis of characteristics of the populations and environmental factors which condition the activity of the population. Attributes of individuals alone cannot predict the functioning of a whole ecosytem; investigations must be focused on population characteristics and chosen ecological factors. (Ciesielska 1978, 1985; Lacey et al. 1992; Loschiavo and Smith 1986; White and Sinha 1980; Sinha 1984).

Data concerning the sex structure of populations of most animals show that the primary sex ratio is close to 1 (Deevey 1947; Kalela and Oksala 1966; Lampio 1965). No influence on the sex of an individual with a chromosomal type of sex determination is possible. Ecological factors can indirectly influence the primary sex ratio in a population by selecting genotypes with tendency to producing offspring of a determined sex predominance (Petrusewicz 1965). However, the sex structure of a population can also be influenced by different migration of males and females after the period of reproduction thus leading to division and formation of groups of different sex ratio.

There is a number of aspects of ecological importance concerning investigations on sex structure of populations. Apart from the possibility of determining the reproductive potential by investigating the directions of changes of sex ratio, the course of dynamics of the population and its activity can also be predicted. From an experimental point of view, populations of grain beetles are very suitable for such model investigations.

Dynamics and activity of populations of *Oryzaephilus surinamensis* (L.), *Sitophilus granarius* (L.), *Sitophilus oryzae* (L.) and *Rhyzopertha dominica* (F.) are described. Observations concerned population density, age and sex structure, interspecific competition, and such environmental factors as food, its lack or distribution and environmental conditions enabling migration. Apart from population dynamics, the tendency to migration and dispersion was analysed to estimate population activity.

The tendency for migration and dispersal was displayed by the insects looking for new habitats and food. These processes intensify with progressing grain exploitation and increase of population density. Based upon preliminary investigations (Ciesielska 1992) a hypothesis was forwarded that age and sex structure exert considerable influence on the migration process.

Material and Methods

Populations of *O. surinamensis*, *S. granarius*, *S. oryzae* and *R. dominica* were studied in single-species and competitive two-species systems. In experiments on migration, *R. dominica* was studied in competition but without any migration possibility. In some of the preliminary experiments, special jars were used, which made the expansion of *R. dominica* possible.

The series of experiments concerned:

Dynamics of populations in various environmental and population conditions, as: different food and different depths of its layer. 2 variants of initial density: 20 individuals (optimal) and 100 individuals (overdensity) for 40 g grain. Long-term experiments concerning the relation between population numbers and sex ratio in single species cultures and in interspecific competition.

Migration and dispersal tendencies of populations in single species systems and interspecific competition. Open jars with grain infested with initial populations in one- and two-species systems (initial density 40 individuals for 40 g of grain) were placed in bigger tightly closed jars. Two experimental variants were applied:

1) unidirectional emigration to jars without any food having a glycerine trap,
2) two-directional migration to jars with an analogical grain content.

Experiments were checked every 30 days according to a previously described method of carrying out long term experiments (Ciesielska 1978). All experiments were conducted at 27°C and r.h. ca 70%. Experiments concerning population dynamics under various environmental conditions were replicated 10 times, the others 20–25 times. Results were based on mean data. The following were calculated: standard deviation, indices of variability, percentage indices of migration and sex ratio. Models of the course of processes were based on statistical analysis of results.

* Institute of Biology, Dept. of Ecology and Environment Protection, Pedagogical University, Podbrzezie 3, 31–054 Kraków, Poland

Results

Population numbers within *S. granarius*, *S. oryzae*, *R. dominica* and *O. surinamensis* are influenced by environmental conditions, intraspecific and interspecific interactions. The decrease in the population number may occur because of an increased mortality rate, decreased oviposition rate and/or decreased developmental rate. Another way of regulating the population number is to change the sex ratio.

A leading factor regulating population number is the different male and female mortality rates at various stages of development of individuals and the whole population. Changes in sex ratio were observed within groups of individuals either surviving or dying at juvenile stages; in conditions of various thickness of the layer of the substrate from favourable conditions to undesirable; in aging populations; with food gradually running out; and finally in interspecific competition (Figs 1,2; Tables 1–3). A wide range of factors facilitated drawing more general conclusions.

The sex structure of a population is not a permanent feature, although the primary structure is generally balanced. It is formed only in subsequent periods of a population's development. The secondary sex structure is correlated with some factors both of the environment and the populations working together. Also at juvenile stages a balanced sex ratio is maintained with the tendency to female dominance. Such a pattern is assumed to be natural to the population of granary beetles. The dominance of females is the reason for the high biological activity and reproductiveness of these species.

A more interesting problem seems to be the development of the secondary sex ratio under conditions of interspecific competition. (Figs 1,2; Tables 1–3). At the final stage of population development in the two species culture where the competition results in replacement of *O. surinamensis* by *R. dominica*, a typical feedback between the fluctuation of the population growth curve and sex ratio occurs (Fig. 2). In the case of *O. surinamensis* and *S. granarius*, however, at the initial stage of the increase of the number of individuals in a population, interactions between these two species in a given set of environmental conditions can be classified as proto-cooperation. In this structure, sex ratios approximate 1, with the tendency towards female dominance for *S. granarius* and male dominance for *O. surinamensis*. At subsequent stages of the population growth the relation between these species converts into a typical competition. It can be stated then, that the process of replacing the feebler population as a result of competition begins with the change of its sex structure.

Earlier research showed that the thickness of the layer of the grain has a considerable importance for *S. granarius* development (Ciesielska 1978), with developmental rate slowed when the substrate layer is too thin. The low number of individuals in the grain from 0.5 to 1.0 cm thick is correlated with dominance of males. After approximately 90 days, the sex ratio ranges from 1.3 to 1.4. However, in a culture where the thickness of the layer of the grain is between 3 and 4 cm the sex ratio does not exceed 0.8 in analogous period of time (Fig. 1, Tab. 3). This indicates the dominance of females.

Summing up, on the basis of this set of experiments, the following can be stated. Under normal conditions, deterioration of living conditions causes the decrease in the population number, which is usually preceded by a change in the population's sex structure towards the dominance of males (sex ratio>1). The increase in sex ratio is caused by dying out of females (in the group of dying-out individuals, the sex ratio is <1). The dominance of female individuals within the population is followed by periods of increase in the population number. Thus, the increase results not only from an increased reproductive rate, which refers to the intensity of reproduction of respective females.

Changes in the sex ratio of a population, occurring due to differential rates of mortality and survival of individuals of opposite sexes, is one way of regulating the population number, especially when the population faces extinction as a consequence of worsening environmental conditions. Deterioration of environmental conditions causes the decrease in a population and also makes the process of change in the sex structure of a population faster. The amount of females decreases. The model of the process is shown in Figure 3.

Activity of population is not only the ability to increase its numbers. It is also reflected by the tendency to disperse. The calculated indices of migration show a high migration and dispersion tendency in all the investigated species. Their values vary according to environmental conditions and system (1- or 2-species) from 40 to over 80 %. Observations on uni-directional migrations to traps showed a high migration activity even during the initial period of infesting the grain. From the populations of *O. surinamensis*, *S. granarius* and *S. oryzae* about 60% of individuals emigrated within the time period from 30 to 90 days. The rest of the population left the initial habitat within the successive 30–60 days. In 60% of replicates all adults of *S. granarius* and *O. surinamensis* left the initial substrate within the first 60 days. In the other experiments the population numbers remained at a very low level for another 90 days.

In 2-species competitive systems migration activity was higher. After 30 days about 80% of individuals left the initial population. This applied to both systems in which the two competitive populations could leave the culture jar as well as the system where only one species was able to emigrate (*O. surinamensis* with *R. dominica*). From the 60th day the population number stabilised at a low level. In 70% of replicates all individuals of populations in 2-species competition left the initial habitat. (Table 4).

Natural environmental conditions were simulated where continuous two-directional migrations (with the possibility to return to the initial habitat) were possible. In this series of experiments too the results showed predominance of emigration processes over immigration ones. The populations numbers of *O. surinamensis* and *S. granarius* in the outer jars was always greater. However, migration activity changes in time. Two periods of peak activity were distinguished: the first is the initial period of inhabiting the grain, and the second after a time lapse of about 180–200 days as a result of grain exploitation and overdensity of population (Table 5).

The population *S. oryzae* showed a tendency to uniform dispersion. This was shown by the emigration index within range of about 50% maintained during the whole investigation period.

Mortality of the initial populations *O. surinamensis* and *S. granarius* was higher as a rule than of the groups of emigrants. In single species cultures, mortality indices in groups of emigrants ranged from 6–15%, and in initial populations they are about twice as high (Table 5).

Analogous results were observed within competitive interspecific systems, at a higher mortality, however. In emigrating groups the mortality was about 15–17% and in initial populations about 60%.

In populations of *S. oryzae*, the relation between migration and mortality was also different. The tendency to uniform dispersion expressed by an equalised migration index was reflected in a uniform course of mortality. In single species cultures, mortality indices in migrating groups fluctuated on average 3.7% and in initial populations 4.1%. In competition systems, mortality indices in groups of migrating individuals

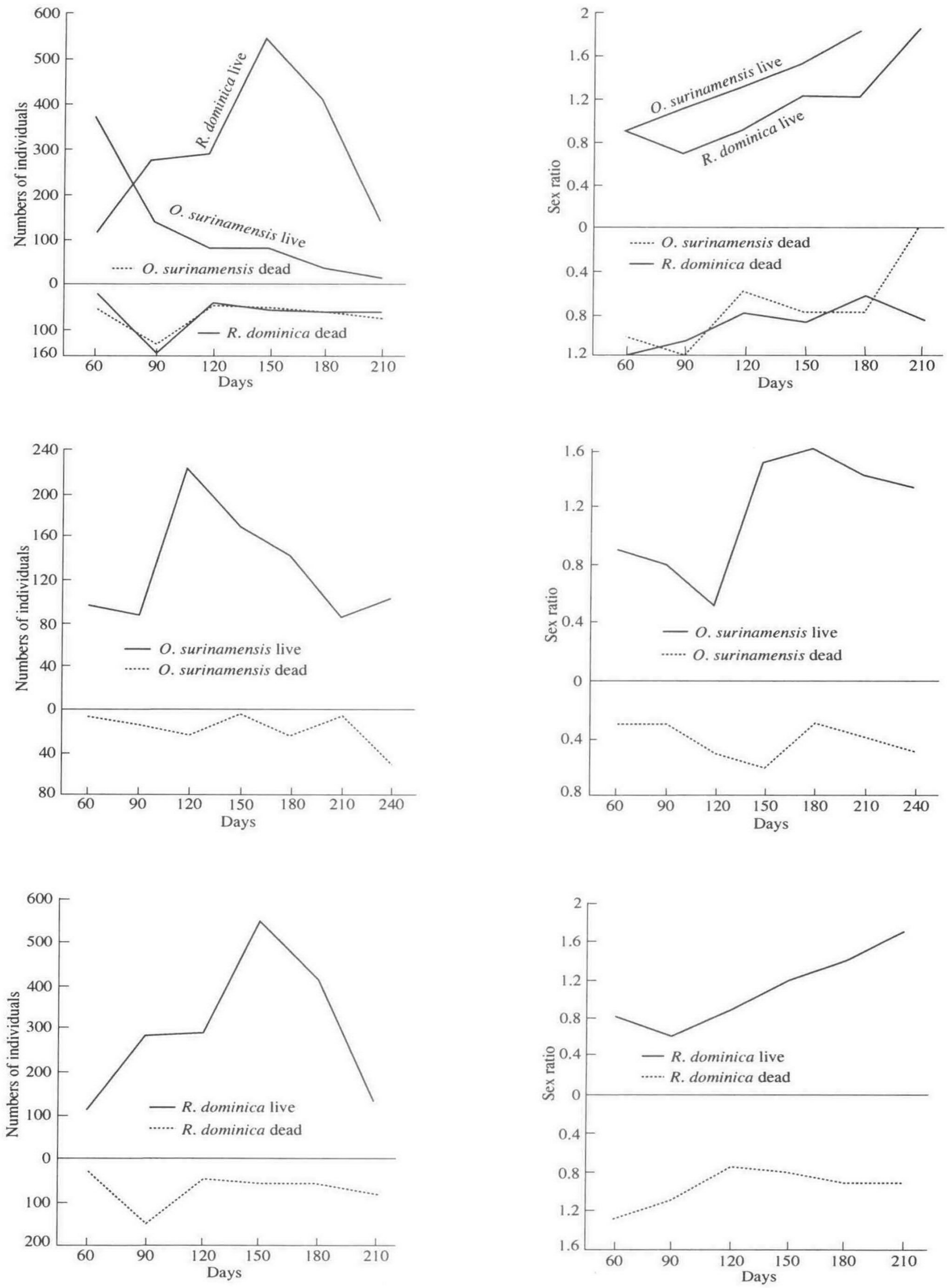

Fig. 1. Changes of numbers of individuals and sex ratio in populations of *O. surinamensis* and *R. dominica* in interspecific competition and in single cultures.

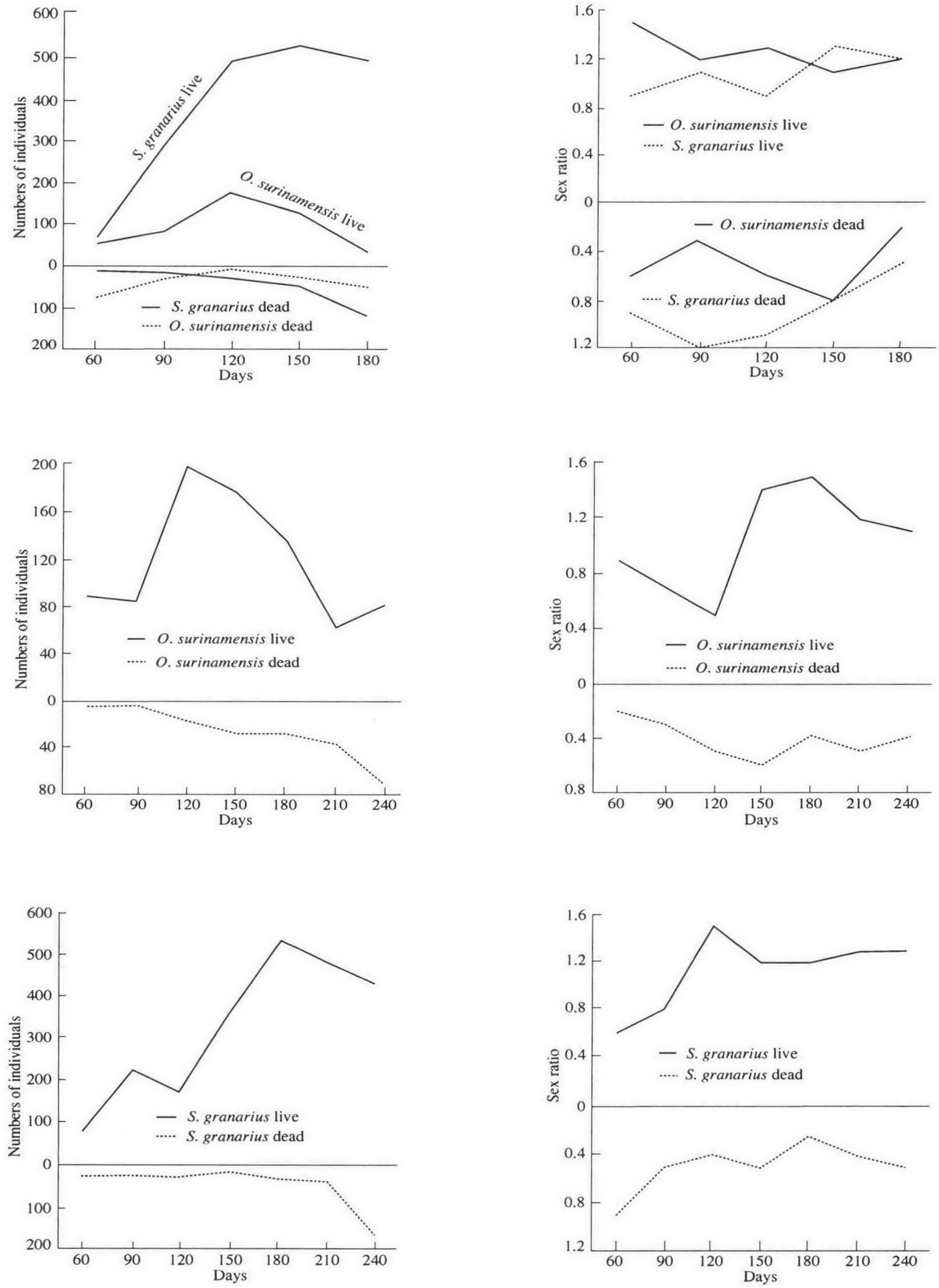

Fig. 2. Changes of numbers of individuals and sex ratio in populations of *S. granarius* and *O. surinamensis* in interspecific competition and in single species cultures.

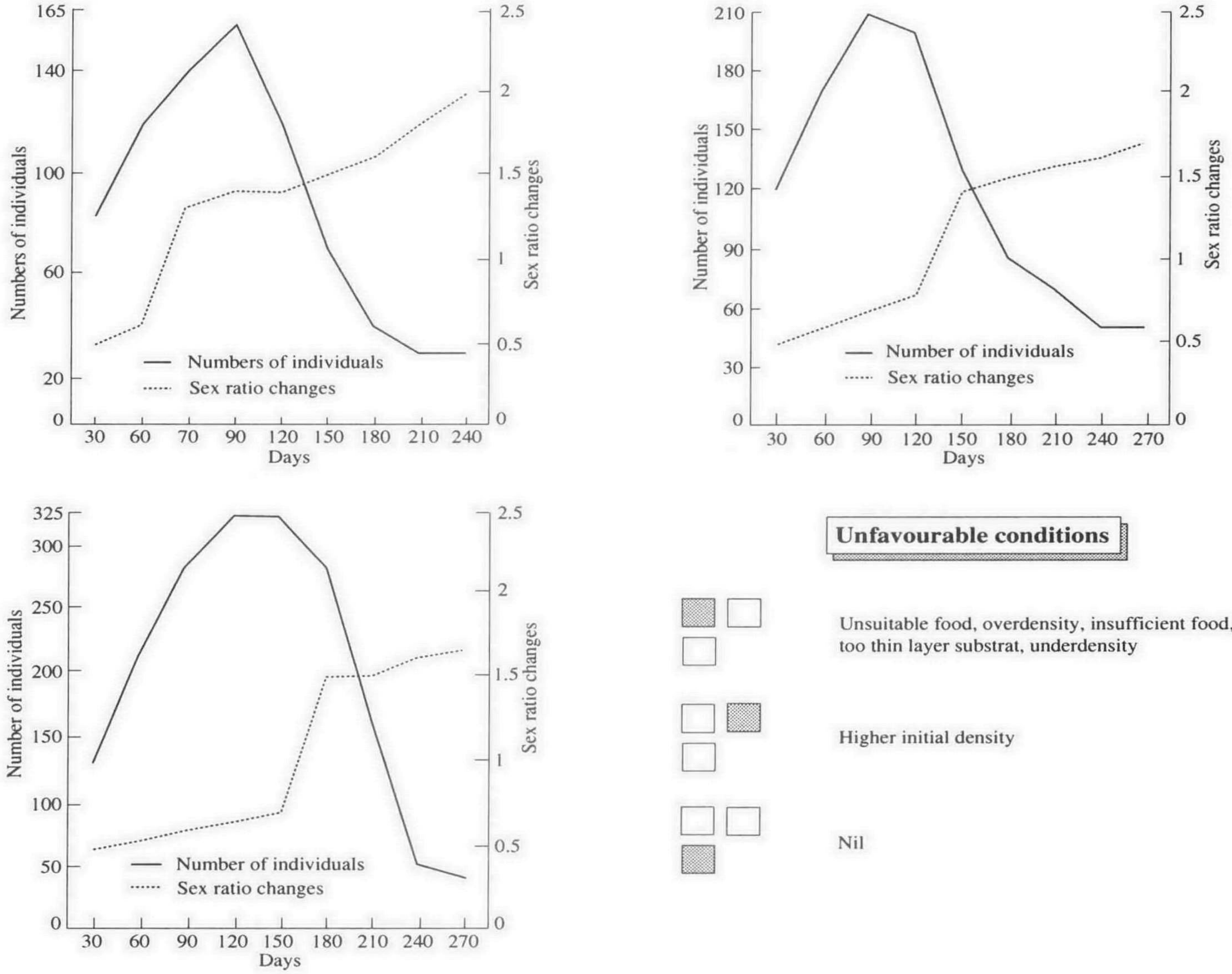

Fig. 3. Sec ratio changes in populations in various environmental conditions.

was on average 40.5%, whereas, in initial populations it was 37.5%.

Two models of migration processes were observed. The first occurred when more active individuals emigrated (maybe younger ones) characterised by a low death rate. In this group emigration processes predominate over immigration processes. The second occurred where uniform dispersion took place, not distinguishing in the population more or less active groups of a higher or lower mortality (Table 5).

The sex ratio of the population is a measure of the group activity and consequently of its value for the development and expansion of the population. Preliminary investigations showed a higher emigration tendency of females (Ciesielska 1992). Continued long term investigations confirmed this result.

The females of the investigated species demonstrated a higher migration activity, confirmed by sex ratio values less than 1 in groups of emigrating adults (Table 5). Highest migration activity was observed in females in the initial period of infestation of the grain (days 30–90). In this time the sex ratio values are from 0.4 to 0.8. The second period with a predominance of females within migrating groups was noticed after the lapse of 180 to 200 days. In this time overdensity of the population and increased grain exploitation took place. The tendency to migrate by *R. dominica* populations was especially high. Previous experiments indicated that females of *R. dominica* are twice as active as males (Table 5).

In competitive systems the activity of females is also higher. It was especially distinct in the situation where *O. surinamensis* was in competition with *R. dominica*. Females of *O. surinamensis* `escaped' from this competitive system extremely actively.

In summary, it should be stated that migration activity of the investigated species led to formation of aggregations or to uniform dispersion. Continuous infestation of stored grain by populations of granary beetles results without doubt from their exceptional tendency to migrate and disperse. Migration is as much a property of a species as a reaction to changing environmental–food conditions and intraspecific and interspecific competition. Various factors condition the migration processes: behavioural–physiological, properties of a species and populations and environmental factors.

Table 1. Sex ratio (males/females) in populations cultivated in various population and environmental conditions

Species	Days	Favourable conditions	Higher initial density	Lack of food, competition	Depth of wheat layer	
					> 3 cm	ca 0.5 cm
O. surinamensis	0-60	0.6	0.7	1.04		
	60-90	0.9	0.9	1.2		
	90-120	0.4	1.2	1.4		
	120-180	1.2	1.3	1.46		
	180-220	1.2		1.1		
	220-		1.3			
R. dominica	0-60	0.53	0.7	0.8		
	60-90	0.69	1.1	1.2		
	90-120	1.1	1.32	1.32		
	120-180	1.3	1.25	1.25		
	180-220	1.09	1.1	1.1		
	220-	1.2				
S. granarius	0-60	1.1	0.7	0.6	0.7	1.6
	60-90	0.7	1.1	0.9	0.9	2.3
	90-120	0.9	0.7	1.4	0.7	1.7
	120-180	1.1	1.3	1.1	1.1	1.5
	180-220	1.5	1.3	1.3	1.1	1.4
	220-250			1.4	1.0	1.2
	250-			1.6		
S. oryzae	0-60	1.0	0.9	1.0		
	60-90	1.1	0.8	0.9		
	90-120	0.9	1.1	1.2		
	120-180	1.1	1.1	0.13		
	180-220	1.1	1.2	1.7		
	220-		1.3	1.6		

Discussion

Both reproduction and mortality are closely connected with the sex structure of the population, usually expressed as the sex ratio. In the majority of species, the sex ratio is approximately 1 during the initial phases of population development. In groups of adults deviations from this ratio can occur differently in different age classes, for example, in *Perdix perdix* or *Lophotortyx californica* proportion of males increases in older classes (Lack 1954). In mammals, sex ratios are close to 1 in embryonic and juvenile stages, with a tendency to deviation from this proportion in adults (Lampio 1965, Kalela and Oksala 1966, Gliwicz 1990). Sex structure of populations can undergo modifications by differentiation of the growth rate or maturity of individuals of one sex.

Predominance of individuals of one sex influences population dynamics. Variability of sex ratio can also be considered from the point of view of influence of certain factors on the rate of mortality of individuals of different sexes. Deviations of the sex ratio from 1 are often the consequence of different survival of males and females as well as different seasonal migrational ability (Deevey 1947, Petrusewicz 1965). Dependence of the sex ratio on density is encountered but this is not the rule. Under low density conditions the predominance of males leads to a decrease of population numbers (Ciesielska 1985, 1988).

Laboratory populations of stored product insects are especially convenient for investigations constituting the basis both for theoretical considerations and practical applications (White and Sinha 1980; Sinha 1984; Loschiavo and Smith 1986; Lacey et al. 1992; Cofie-Agblor et al. 1992). The first part of investigations, showed that the main factor regulating population numbers is differential survival of males and females at various ages and periods of population development (Ciesielska 1978, 1988). Based upon very numerous experiments and replicates, changes of the sex ratio were analysed within dying-out and surviving groups of individuals, in juvenile stages, in conditions of various densities, at lack of food and its overabundance, in favourable and unfavourable conditions of food distribution (depth of the substrate layer), and in ageing populations connected with gradually decreasing of food.

A multidirectional analysis of the problem permits some general conclusions. Sex structure of a population is not its constant property, although the primary structure is equal as a rule. Changes occur only at later developmental stages of the population. The secondary sex structure is correlated with environmental and population factors acting jointly.

When environmental conditions are poor, the decrease of population numbers is preceded by a change in sex structure tending to favour males. Increase of the value of the sex ratio (>1) takes place by means of increase of mortality of females. A higher participation of females in a population (sex ratio <1) preceded periods of increase of population numbers. Thus, it is the effect not only of an increase of the reproductive index value determining the biotic potential of a population but also of the sex structure. In all the investigated populations of grain beetles not endangered with unfavourable environmental conditions, a tendency to a higher proportion of females prevails.

Table 2. Sex ratio (males/females) among adults dying out in populations cultivated in various environmental conditions

Species	Days	Favourable conditions	Higher initial density	Lack of food, competition	Depth of wheat layer	
					> 3 cm	ca 0.5 cm
O. surinamensis	0-60	0.5	0.4	1.33		
	60- 90	0.3	1.1	1.12		
	90-120	0.6	0.6	0.42		
	120-180	0.5	0.7	0.69		
	180-220	0.4	0.8	0.34		
	220-	0.4	0.7			
R. dominica	0-60	0.3	0.33	1.25		
	60-90	90	0.4	0.9		
	90-120	0.3	0.09	1.3		
	120-180	0.8	0.62	0.7		
	180-220	0.6				
	220-					
S. granarius	0-60	1.0	0.4	0.9	0.6	0.3
	60- 90	0.5	0.8	1.7	0.5	1.3
	90-120	0.7	0.8	1.2	0.4	1.6
	120-180	0.8	0.6	1.1	0.8	1.0
	180-220			1.0	0.6	3.3
	220-250			0.8	0.4	1.7
	250-1.0			1.0		
S. oryzae	0-60	0.3	0.4	0.9		
	60-90	0.5	0.5	0.8		
	90-120	1.3	0.6	1.0		
	120-180	1.6	0.3	1.1		
	180-220	0.4	0.8	1.0		
	220-	0.9				

Table 3. Sex ratio (males/females) in *S. granarius* populations in various initial density and depth of layer of wheat

Adults	Depth of wheat layer							
	ca 0.5 cm				ca. 3.5 cm			
	Initial density				Initial density			
	100 ind	S.E.	20 ind	S.E.	100 ind	S.E.	20 ind	S.E.
Live	1.85	0.43	1.25	0.81	0.80	0.02	0.83	0.27
Dead	0.70	0.25	1.35	1.12	0.76	0.11	0.60	1.20
Total	1.227	0.67	1.30	0.97	0.78	0.60	0.61	0.68

Directional change of the sex ratio occurs by differential mortality and survival of individuals of different sexes and is one of the ways of regulating the population numbers during times when the existence of the population is endangered due to deterioration of environmental conditions.

On the other hand, a higher activity of females expressed by their higher proportion in groups of emigrants assures population emigration success. In populations of grain beetles this is enhanced by a lower mortality within groups of emigrating individuals.

Dispersal behaviour of animals has been investigated under natural and laboratory conditions (Surtees 1965, Lidicker 1975). Investigations on the emigrating behaviour of natural populations of Microtinae (Gliwicz 1988, 1990) showed that mortality in groups of migrants is higher. Differences in relation to data obtained for populations of grain beetles do not only result from differences of taxonomy groups and laboratory investigations. Investigations of Gliwicz concern small mammals whose high mortality takes place mainly during searching for new areas. Whereas, after finding such areas the reproductive success is often higher than in initial populations. Hence, the problem whether the migration behaviour brings profit only to migrants or to the whole populations is still disputable. It seems that emigration improves conditions also to these individuals which do not leave the donor habitat by decreasing population density. Tschinkel (1981) suggested that larvae of *Zophobas atratus* showed an increasing tendency to overdispersal as the density of the population increased.

In conclusion, it should be stated that migration behaviour developed in response to both physiological and ecological factors. Hence, the course of the process is the result of their influence. The established high tendency to migration and dispersion in populations of the investigated species of granary beetles and especially high migration activity of females is a direct cause of their continuous expansion.

Table 4. Indices of migration (means only presented)

Days	*O. surinamensis*		*S. granarius*		*S. oryzae*	
	Single species	In competition	Single species	In competition	Single species	In competition
Undirectional emigration to traps						
30–90	59	78	62	81	56	68
90–150	40	26	35	14	38	23
Two-directional migrations						
30–90	78	88	81	72	58	68
90–150	59	64	72	69	48	51
150-210	64	65	67	59	48	57
210+	84	78	79	81	58	61

Table 5. Sex ratio (males/females) and mortality

Days	*O. surinamensis*		*S. granarius*		*S. oryzae*	
	Initial population	Migration groups	Initial population	Migration groups	Initial population	Migration groups
Single species culture: sex ratio						
30–90	1.4	0.4	1.1	0.7	0.7	0.9
90–150	1.6	0.8	0.9	0.5	0.7	0.7
150-210	1.4	1.0	1.1	0.9	0.8	0.9
210+	2.1	0.8	1.4	0.6	1.4	0.8
Mortality %						
30–90	23.9	6.2	13.0	6.8	1.9	2.9
90–150	32.6	3.7	15.9	11.8	6.2	7.6
150-210	18.7	10.6	31.8	9.7	5.3	2.4
210+	36.0	14.7	37.1	12.9	3.3	2.1
In competition: sex ratio						
30–90	1.5	0.5	1.2	0.8	1.0	0.8
90–150	2.0	0.9	1.1	0.6	0.9	1.0
150-210	1.2	0.6	0.9	1.0	1.1	0.6
210+	1.4	1.1	1.3	0.9	0.9	0.8
Mortality (%)						
30–90	64.4	1.2	14.2	13.3	24.0	43.3
90–150	55.0	13.8	12.5	10.8	39.7	56.3
150-210	84.1	17.6	35.3	22.6	34.7	37.9
210+	53.8	28.2	41.2	27.1	42.2	33.0

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